

THE DIGESTIVE SYSTEM OF THE PERIODICAL CICADA, TIBICEN SEPTENDECIM LINN.

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I. INTRODUCTION.

Numerous authors have reported the impossibility of following the digestive system of the periodical cicada throughout its entire length. Of those who state that it is complete and well organized, none attempts any detailed description. My attention was called to the matter in 1916 by Dr. C. W. Hargitt who had himself been interested in the question of digestive activity in this insect for some years. Dr. Hargitt's observation dealt particularly with the feeding habits of the cicada. He had also directed a graduate student, R. L. Henderson, in an attempt to work out the morphological details of the enteron. Unfortunately before this work was completed the death of Mr. Henderson intervened.

In the present work I have constantly consulted with Dr. Hargitt, but the entire responsibility for the morphological details herein presented lies with me. A further publication, in which Dr. Hargitt has the major interest, dealing with the physiological aspects of the problem, will appear shortly.

II. LITERATURE.

There has been much lack of agreement in the literature as to whether the cicadas do or do not feed and this question has led in turn to the inquiry as to whether the digestive tube is atrophied in the supposed cases of non-feeding. Marlatt (1898) in his summary of the habits of the insect, says that during its aerial existence "it seldom, if ever, takes food." In

another place he says that feeding is limited to the female, the digestive system of the male being rudimentary.

Quaintance (1902) made a series of careful observations upon the brood which emerged in Maryland during the early summer of 1902. He was able to find numerous insects, both male and female, apparently feeding upon the branches of young fruit trees. He snipped off an insect's proboscis while the latter was embedded in the bark of a twig and shows a photograph of a section of this bark pierced by the setæ. He states that he found that the alimentary tract was not rudimentary in either sex, although he attempts no description nor gives any figures to prove his statement.

Hargitt (1903) suggested that there seems to be a complete atrophy of the hind gut at the time of emergence while the mid-gut undergoes an increase in size until the abdomen is almost entirely hollow. He suggests that this condition represents an adaptation enabling the insect to make use of the stored fat, using this food to the exclusion of plant juices.

Marlatt (1907) in a revision of his earlier bulletin corrects his former statements regarding the feeding habits of the cicada. He is convinced of the possibility of feeding by the observation of Quaintance, but still questions whether the cicada necessarily takes food.

In an unpublished paper by R. L. Henderson, under the direction of Dr. Hargitt, to which we have had access, numerous observations were recorded which have proven valuable in this study. Although Henderson did not work out the digestive system completely, his account shows that he had identified and traced the course of certain parts of the canal.

Dufour ('33) describes and figures the digestive system of *Cicada orni*. In general his findings are very similar to those here presented for *Tibicen septendecim*, except that he did not recognize the complication of crop and "internal gland." According to Dufour the esophagus dilates posteriorly to make the crop. The crop continues into the "poche du ventricule chylifique." Then follows a smaller much-coiled tube which finally runs forward, apparently emptying into the anterior portion of the "ventricule chylifique." The crop gives off a lateral diverticulum which continues posteriorly as a narrow, much-coiled tube and finally empties into a short rectal division which ends at the anal opening.

From the above it is evident that there is no agreement as to the necessity of feeding in the adult insect nor has the morphology of the digestive system been worked out sufficiently, in *Tibicen septendecim* or any closely related forms, to warrant inferences as to functional activity based upon structural conditions.

III. MATERIAL AND METHODS.

The observations herein recorded are based upon the periodical cicada, *Tibicen septendecim* Linn. Numerous specimens of the so-called dwarf cicada have been collected, but they were not used in this work. Material was collected during June, 1916, by the author in the vicinity of Syracuse. Additional insects were gathered near Moores Hill, Indiana, by Dr. A. J. Bigney.

The material was fixed in the following fluids: Bouin, 10% formol, sublimate acetic, Gilson, potassium dichromate, and Zenker. In order to insure rapid penetration of the fluids, the integument was slit with a razor on the ventral side, or the head was cut off allowing the fluids to penetrate rapidly from the anterior end.

Dissections of freshly killed and also of preserved insects were made under the binocular microscope. The dissection method was not sufficient to reveal all of the relationships of the digestive organs so that serial sections of entire insects, as well as of parts of the digestive tube with adhering tissue, were made.

In making serial sections of entire insects it was necessary to soften the chitinous integument by means of Labarque's solution. After this process the insects were embedded by the double method of Apathy and sections were cut ten microns thick. Such sections were valuable only for determination of general topographical relationships.

The various digestive organs were dissected out and serial paraffine sections 5 microns thick were made in the usual manner. They were stained with hematoxylin and eosin. By means of these sections various relationships were made apparent which could not be cleared up by gross dissections.

IV. THE DIGESTIVE TUBE IN THE ADULT MALE INSECT.

The male has been chosen as the subject for more detailed description because of the fact that in this sex particularly more doubt has been expressed as to the completeness of the enteric canal.

In the cicada it is difficult to recognize the boundaries of the fore, mid and hind guts. Not only do these parts fail to conform in their gross anatomy to the relatively simple divisions as found, for example, among the Orthoptera, but their histological structure also fails in most cases to correspond with that of the more familiar forms. The puzzling relationship of parts and the changes taking place in some of these parts during the life cycle may be due to any or all of several factors, viz., the nature of the liquid food; the influence of food stored in the body in the form of fat; or to the peculiar life history of the insect. However, since most of the sap-sucking Hemiptera in which the digestive apparatus has been described have some similar peculiarities, no clue is obtainable from them as to the significance of these conditions. That part of the following description relating to the sequence of parts in the tube and to their general relationships can best be understood by reference to Fig. 3. This is entirely schematic and attempts to represent none of the finer details of structure.

The extreme anterior portion of the digestive canal is not greatly different from that described for numerous other forms. The long proboscis, containing a pair each of functional stylet-like mandibles and maxillæ, leads dorsally through the pharynx into the narrow esophagus. The latter, when it reaches a point midway between the dorsal and ventral surfaces of the animal, turns at right angles and proceeds toward the posterior end. The point where the esophagus changes direction is just posterior to the boundary between the head and prothorax.

The esophagus does not vary much in diameter throughout its entire extent, (Figs. 2 and 3). It may, with little difficulty, be followed in a properly dissected specimen, with the unaided eye, and it is easily traced with a lens of low magnification. At the line of division between the mesothorax and the metathorax the esophagus empties into the crop.

The crop is divided into two parts of unequal size. The anterior part (Figs. 1, 2 and 3, ac) is the smaller and is usually

confined to the metathorax. The posterior portion (Figs. 1, 2 and 3, pc) has its anterior boundary at the beginning of the first abdominal segment. Its extent in the posterior direction is variable and this variation will be discussed later but in extreme cases its posterior boundary is found as far back as the sixth abdominal segment.

The dorsal wall of the anterior crop is concealed by a winding mass of tubes which will be described later. For want of a better name this mass will be called the "internal gland," following the terminology of Lubbock ('59). Although Lubbock probably intended his designation to include more than it does in the present case, it seems expedient to continue the use of the term in connection with that part of the complex made by the ascending intestine and malpighian vessels just above the anterior crop. In shape, this complex of crop and internal gland usually appears as an elongated spheroid, but it may be bent upwards so as to look in side view like an inverted U. The diameter of the entire structure is roughly five times that of the esophagus. Posteriorly it narrows and apparently connects with the large posterior crop.

The descending intestine arises from the left side of the internal gland near its anterior margin. In a gross dissection this tube sometimes appears to be a continuation of the esophagus but sections of this region show it to be otherwise, as will be explained later. It is only about half the diameter of the esophagus and is characterized by a gray color which is uniform throughout its whole extent. It follows the ventral margin of the anterior crop but leads in a general posterior direction. The windings of this tube are confined in most cases to the dorsal half of the insect. At the boundary between the sixth and seventh abdominal segments it winds upon itself in such a way as to make a knot (Figs. 1, 2 and 3, kk). From this knot or coil the tube emerges and joins the rectum which latter narrows as it passes posteriorly until it ends in the anal opening.

The posterior end of the internal gland receives another tube (Figs. 1, 2 and 3, at) which is distinguishable from the one previously described both as to its color and also with regard to the course it takes. Its color is noticeably yellow, a condition as will be shown later, traceable to the presence of cytoplasmic inclusions in the epithelium of its walls. This yellow tube, the ascending intestine, also runs in a sinuous fashion over the sur-

face of the posterior crop but is chiefly confined to its ventral surface. Following the intestine backward it may be traced to the posterior boundary of the sixth abdominal segment where it takes a dorsal course toward the rectum. As in the case of the descending intestine, a knot or coil is formed (Figs. 1, 2 and 3, k) but when the tube emerges from the coil, it turns anteriorly and connects with the posterior crop at the extremity of the latter (Figs. 1 and 2, x).

The posterior crop is one of the most puzzling divisions of the tube at first sight. It is enormously developed, especially in the adult male during later life, and its gradual enlargement from the period of emergence to late life is one of the anomalies demanding adequate explanation. Because of the thinness of parts of its walls its true nature might be unsuspected if one depended upon gross dissections alone. In the adult male it extends from the metathorax to the end of the sixth abdominal segment (Figs. 1, 2 and 3, pc). An anterior cæcal prolongation extends forward beneath the crop as indicated in Fig. 3. Its main portion gradually enlarges posteriorly except for indentations at the boundaries of one or two segments until, beginning in the region of the second abdominal segment, its walls closely approximate the chitinous integument on all sides. The small intestinal tubes connecting fore and aft with the internal gland run their courses upon its outer surface as indicated above.

The rectum is confined usually to the last two abdominal segments (Figs. 1, 2, 3, r). It is an elongated sac with numerous longitudinal folds and lies close to the dorsal integument. It is easy to understand how some writers may have gotten the impression that the digestive tube of the male insect did not have any complete posterior portion, for in all cases where a dissection is attempted from the dorsal side the rectum is destroyed. It is practically impossible to remove any part of the dorsal integument in this region without injuring the underlying rectal sac. It can be exposed, however, by carefully dissecting from the ventral side, through the mass of coiled reproductive ducts and fat.

The foregoing description is based entirely upon observations in the adult male insect. While the female organs are arranged on the same general plan, there are slight variations and these will be mentioned in another place.

From what has been said it should be apparent that the adult male cicada possesses a digestive tube which is most peculiar both with respect to elements which compose it and to the manner of their arrangement. It is possible to demonstrate by dissections alone, that this insect has a complete and continuous digestive tube yet this fact has been denied by many, and even when admitted, the arrangement and connections of the organs have been imperfectly understood. The relationships of the various parts described must depend upon the study of sections, for it will shortly appear that certain apparent connections between elements as indicated in whole preparations are indeed apparent and not real.

RELATIONSHIPS OF THE DIGESTIVE ORGANS.

As suggested above, the connection between the various parts of the digestive system are not very clear in gross dissections. The actual union of some of the different divisions of the system can be clearly demonstrated only in sections.

With the view of determining the true nature and relationships of parts in the anterior part of the digestive tube, the crop with the internal gland was dissected out of numerous adult insects. Transverse, sagittal and frontal sections were cut, and by means of these the independence of crop and internal gland was established. A median sagittal section of the anterior part of the tube shows that the esophagus is separated from the crop by a valve and that the anterior crop then continues in a posterior direction. As it proceeds, however, its walls become much modified, the floor being greatly thickened, while the roof is relatively thin and much folded. The folds in the roof are very pronounced and run in a general antero-posterior direction. This condition results in the formation of deep external fissures on the dorsal surface of the anterior crop, the ascending intestine and malpighian vessels each being enveloped by the walls between two adjacent folds. These relationships may be understood by reference to Fig. 9, which is a transverse section through the anterior crop region. The same structures are also represented diagrammatically in Fig. 6.

This modified anterior crop upon reaching the posterior portion joins directly with the latter. The aperture leading into the posterior crop is small and irregular by virtue of the convoluted walls of the connecting portions. While the dorsal

wall of the anterior crop is thin and has its epithelium poorly developed, this does not imply that there is any connection with the tubes which coil above this region. The anterior crop receives no tube, other than the esophagus, nor does it give off outgrowths in any part.

It was stated previously that the descending intestine, arising from the left anterior part of the "internal gland," looks, in a dissection, as if it might be a posterior continuation of the esophagus. Sections do not confirm this possibility. On the contrary, a frontal section (Fig. 7) shows the descending intestine to be continuous with the ascending intestine. The latter enters the internal gland posteriorly and runs forward to its anterior margin. A comparison of sections in three different planes proves, then, that the enlargement in the metathorax is composed of two distinct parts—a dorsal, tubular, closely-wound mass made by the ascending intestine and malpighian vessels, and a ventral distensible portion continuous with the esophagus.

The posterior crop neither receives nor gives off any outgrowths until its extreme posterior end is reached. Sections show (Fig. 14) that it empties directly into the narrow ascending intestine which then proceeds in a general anterior direction to join in the formation of the internal gland, as previously described. A muscular ring or valve is found at the junction of the last mentioned parts.

There are four malpighian vessels. They are easily found in any section between the crop and rectum. They are not easily distinguished in dissections since they are almost the same in color as the fat which surrounds them. Their diameter is about half that of the intestine. The blind ends of the tubules lie in the extreme posterior end of the body. They run forward in irregular fashion, mostly dorsally, until they approach the region of the anterior crop. Here they describe a short loop just above the internal gland and then disappear into it at its posterior margin.

From the foregoing descriptions it is clear that if plant juices are taken in as food, they are conveyed to the anterior crop directly through the esophagus. They then pass to the posterior crop which, in all probability, functions as a storage sac as well as contributing to the digestive process. From the posterior crop the liquid food passes into the ascending

intestine through which it goes anteriorly until it reaches the internal gland. After traversing the latter it again starts in a posterior direction through the descending intestine and finally enters the rectum, the last organ of the system. There seems to be no possibility that the food material takes any other course than that outlined above. There are no connections between the parts described which would permit any other course, and the presence of valves shows that the food stream could follow only the direction outlined.

HISTOLOGICAL STRUCTURE OF THE DIGESTIVE ORGANS.

The Esophagus.

The epithelium of the esophagus has no prominent cell boundaries. Here and there can be seen cells whose free margins are separated by walls, but for the most part the epithelial lining appears as a syncytium. The nuclei are prominent, being large and containing numerous chromatic granules rather evenly scattered. The nuclei do not all lie near the proximal ends of the cells, but appear near the distal border as well.

The cytoplasmic portion shows no differentiation between basal and free ends, but is uniformly made up of fine granules or minute fibrillæ which seem to compose the more solid portion of the cytoplasmic mass. Here and there are found vacuolar spaces within the cytoplasm, but in no place does one find cytoplasmic inclusions which could be considered as evidence of secretion or absorption. The latter statement is based upon observations upon sections from numerous insects of different ages in which a wide variation as to activity in feeding was possible. The free margin of the epithelium is bounded by a definite wall, but there does not appear to be any cuticula or striated border. The epithelium lining the esophagus would seem, from these observations, to have a purely passive function, conducting the food material posteriorly, but not contributing otherwise to the digestive or absorptive processes.

The cells of the esophageal epithelium have a well developed basement membrane. Connective tissue elements thicken this in places (in the middle of the folds, for example) in such a way that the folds seem to have a dense core of darkly staining material in which the details of structure do not show them-

selves plainly. This layer of connective tissue elements may be traced entirely around a transverse section.

Adjoining the basement membrane are found two or three layers of muscles—an inner longitudinal and an outer circular layer. The longitudinal layer is not well developed, but consists of scattered bundles of fibres which fit into irregularities at the bases of the epithelial folds. Each muscle is composed of from one to a dozen fibres. The poor development of this layer would suggest that it has little if any functional importance. The circular layer is better developed. It consists of several strata of striated muscle fibres which interweave, making a network (the individual fibres do not branch), which surrounds the tube. Muscle nuclei are not prominent in the layers, but the fibres are easily seen and studied.

In many parts of transverse sections other groups of longitudinal muscle fibres are found outside the circular layer above described. These are numerous and well developed in contrast to the longitudinal layer lying at the base of the epithelium. Inasmuch as the esophagus lies between the large thoracic muscles which attach to the appendages, it is likely that the last described elements are members of this thoracic muscle mass.

The succession of layers above described corresponds rather closely to that in the esophagus of other insects. There is, therefore, nothing remarkable about this organ in a structural sense.

The lumen of the esophagus is continuous with that of the anterior crop through a narrow passageway running between well-developed epithelial folds. These folds have at their bases circular muscles and much connective tissue. A longitudinal section of this region shows that this arrangement is a real valve with a sphincter. It must, therefore, function in preventing the flow of juices back into the esophagus once they have arrived in the anterior crop cavity. On the esophagus side of the valve the epithelium is not folded but gives a funnel shape to the lumen as it runs posteriorly. On the crop side, however, the epithelial lining is thrown into numerous folds (Fig. 10), especially at the point nearest the actual opening in the valvular structure. Liquid going in the wrong direction would thus be hindered in its progress by the folds and a con-

traction of the sphincter would so close the lumen as to prevent effectively passage of any liquid.

The Anterior Crop.

The esophagus empties into the anterior crop through the narrow opening described above. The walls of this division are not uniformly differentiated (Fig. 9). The floor of the organ is so constructed as to permit little expansion. The roof is much folded, the folds apparently allowing some distension as a result of the pressure of the contained liquid food. These differences of structure are easily observed in either longitudinal or transverse sections.

The epithelium covering the floor of the anterior crop is made up of columnar cells varying somewhat in length. Anteriorly its surface is thrown into a series of gentle folds (Fig. 8). The folds increase in height until in the extreme posterior end they much resemble the gastric crypts of some of the vertebrates. The cell boundaries, easily seen in the distal portions of the cells, become less sharply marked as the base of each cell is approached. The cytoplasm of the cells is uniformly granular or homogeneous. No vacuoles or secretion products were observed. The nuclei are large and chromatic and they may be found in almost any position between the base and free ends of the cells. No cuticula or striated border was observed, the free ends of the cells having membranes similar to those covering the basal portions.

The roof of this division has an epithelium much different in character from that above described. The cells are more cubical than columnar. The dorsal folds are very deep (Fig. 9) while secondary folds branch off from the one or two large primary ones in such a fashion that in transverse section the pattern formed resembles the branches of a tree. There is a pronounced cuticula developed upon the surface of the dorsal epithelium.

Cross sections through any part of the anterior crop region show the ascending intestine and malpighian vessels to be closely apposed to the dorsal wall of this organ. These tubes lie in the depressions between the folds previously described but do not actually penetrate the folds at any point.

The entire mass formed by anterior crop and entwined tubes is covered with a peritoneal membrane together with some muscle fibres. The resulting saccular appearance and the

apparent unity of the structure as viewed externally, together with its likeness to glandular tissue as seen in section accounts for the name "internal gland" applied by other authors. The term is retained here only as a convenient designation and for want of proper name which will suggest its real anatomical or physiological nature.

The passageway between anterior and posterior crop is small and irregular in outline. Both divisions of the crop are much folded in a longitudinal direction at their point of junction. This makes a narrow, tortuous connection, at least when the two parts are not distended with food. The circular muscles in this region are not well developed so that there does not appear to be any valvular apparatus for the separation of the two cavities.

The anterior end of the second division of the crop has its walls much folded. These folds are so close to each other that the lumen is a mere irregular slit. The epithelium in this region is not greatly dissimilar to that found in the floor of the anterior crop. The muscles in the walls of the posterior crop are arranged in an inner circular layer which is thin and evenly disposed, and an outer longitudinal layer whose fibres lie in scattered groups close to the circular layer.

In the anterior portion of the posterior crop the epithelial cells are packed with oval brownish inclusions similar to those found in the ascending intestine, described later.

In the middle portion of the posterior crop the epithelium thins out to such an extent that it forms the thinnest of lining membranes (Figs. 12 and 13). The cells lose their columnar character and become cuboid or even squamous. Cell boundaries are indistinct or entirely lacking. The free border of these cells has a striated zone beneath which is a narrow dense layer of granular cytoplasm followed by colorless alveolar substance which is probably made up of small vacuoles filled with fluid. The proximal portions of the cells are filled with a finely granular protoplasm. The muscle layers are not well developed although they may be demonstrated in certain places.

In the posterior end of the posterior crop the epithelium becomes somewhat thicker, especially so at the point where the ascending intestine connects with it. Here again the cells show the yellow inclusions which look somewhat like oil droplets. These are similar in appearance to those found in the most anterior portion.

The opening from posterior crop into the ascending intestine is surrounded by a sort of transitional epithelium. Here the cells are tall and closely packed. They are thrown into slight folds (Fig. 14) but not to the extent found in some other portions of the digestive epithelium. There is a well-developed layer of circular muscles at the place where the tube arises, presumably a sphincter or valve, guarding the opening into the ascending intestine.

The Ascending Intestine.

The ascending intestine, in histological structure, shows great difference from the parts previously described. The lining of this tube is composed of a single layer of irregular epithelial cells which, when fully developed, are very large (Figs. 15 and 16) and have a prominent, centrally-located nucleus. Of all the digestive epithelia thus far considered, that of the ascending intestine seems to be most active. The cytoplasm at the base of each cell is granular, but as the free end of the cell is approached large globules are developed (Fig. 16). When the globules are not present, vacuoles of varying sizes are found in the protoplasm near the distal ends of the cells (Fig. 15).

The nuclei of the large fully-developed epithelial cells become vacuolated just previous to secretion. At the bases of the larger cells are found numerous small replacement nuclei which suggest the method by which new cells are formed to take the place of those cast off. In Fig. 17 the lighter colored cells are apparently in process of developing to replace those destroyed by secretory activity, while the darker ones are about to secrete. The free margin of the cells is bounded by a well-developed striated border. This is so prominent that at certain times it gives the cells the appearance of being clothed with short cilia.

The epithelial cells lining the entire tube from its place of origin to the point where it goes into the internal gland show signs of functional activity of the sort above mentioned. Figs. 15, 16 and 17 represent different phases of the secretory process.

At the base of the epithelial layer is a thin stratum of circular muscle fibres. In some places this is hard to distinguish from the basement membrane of the epithelial cells.

Just outside of the circular muscle layer scattered bundles of long muscle fibres are found. This incomplete long muscle layer is not different in character from that described for the anterior crop.

The Malpighian Tubules.

The walls of the Malpighian tubules are made up of a single layer of cuboid cells. The nuclei of these cells are large and sometimes irregular. The cytoplasm is granular or alveolar depending upon the phase of the secretion process. A well developed intima is present in the cells. In certain places a tubule may be made up of enormous cells placed end to end, in which case there is a single large intracellular duct into which drain numerous smaller ducts which ramify in the cytoplasm in a lateral direction.

At the point where the tubules enter the "internal gland" there is an abrupt change in the character of their walls. They become thin, the nuclei decrease in size and are less chromatic. They retain this membranous character until they finally empty into the intestine near the anterior margin of the "internal gland," at the junction of the ascending and descending intestine.

The "Internal Gland."

As previously explained, the name "internal gland" was used by Lubbock in 1859 to denote the closely wound knot formed by a part of the digestive tube in the thoracic region of certain Hemiptera. The term is here used to designate the complex formed by the ascending intestine and malpighian vessels dorsal to the anterior crop.

The ascending intestine, after running almost the entire length of the abdominal cavity, in the manner previously described, begins a series of coils just above and closely apposed to the dorsal wall of the anterior crop (Fig. 3). Immediately before entering this coil the diameter of the tube becomes somewhat enlarged and there appears to be much secretory activity on the part of the cells of its epithelial lining for they are much vacuolated both as to cytoplasm and nuclei and the free ends of the cells become cast off into the lumen to a greater extent than in the cells nearer the end where the tube originates.

The tube then becomes closely wound upon itself and as it proceeds forward lies close to the wall of the anterior crop. Signs of functional activity are not as pronounced as the tube is followed forward. The cells contain few or no secretion bodies or vacuoles. Cell particles also cease to be cast into the lumen of the tube.

The malpighian tubules accompany the ascending intestine forward contributing a large percentage of the mass of the "internal gland." Their walls become extremely thin while the lumen of each vessel increases greatly in size. These conditions are represented in Figs. 7 and 9 mt.

The Descending Intestine.

While the ascending intestine emerges from the internal gland its epithelium becomes markedly changed. The cells are low and flat and contain no cytoplasmic inclusions. As the tube leads posteriorly the epithelial lining takes a transitional form. This point marks the entrance of the malpighian vessels and the junction of the two intestinal divisions.

The descending intestine is lined with a single layer of large epithelial cells. Anteriorly these cells are vacuolated (Fig. 18), but in the middle and posterior parts the cytoplasm is uniformly granular (Fig. 19). The lumen of the tube is irregular in outline by reason of the triangular shape of the limiting cells. These cells are bordered by a zone of cytoplasm much denser than that found centrally. This dense peripheral zone is distinguishable in the basal parts of the cells next to the underlying muscles as well as at their free borders. This condition reminds one strongly of the ectoplasmic and endoplasmic zones in protozoa.

The nuclei of these cells are large and centrally placed and contain many coarse chromatic granules. Nucleoli do not appear nor are the nuclei vacuolated as was the case in the ascending intestine. The cytoplasm surrounding the nucleus is finely granular or fibrillar, except in the region immediately following the emergence from the internal gland (Fig. 18). Here both cytoplasm and nucleus may show vacuoles. It is to be noted that here also the vacuolation is not accompanied by the modification of the outer zone of protoplasm as previously described.

A comparison of sections of the ascending and descending intestine shows that their color is due to the histological structure of the cytoplasm in each case, the yellow color of the former being caused by the numerous inclusions. The complete absence of these in the descending intestine results in a color difference which enables one to recognize this tube with the naked eye.

The Rectum.

The rectum is relatively short and its diameter is much greater than that of any part discussed thus far except the posterior crop. Its walls are also much thicker than those of any other part of the digestive tube. The epithelial lining is similar to the esophageal epithelium in that the columnar cells are narrow, closely packed, thrown into numerous small folds, and the cell boundaries are indistinct. The muscle layers do not have their fibres running in strict longitudinal and transverse directions, but there are many strands of muscle material running in criss-cross fashion so that a sort of woven mat of tissues makes up the muscular part of the rectal walls. In places, however, distinct layers may be seen, an inner thin longitudinal layer and an outer thick circular layer. The muscle is of the striated variety in both layers and is gathered into typical bundles. The great thickening of the circular layer is not surprising in view of the functional activity of this layer in emptying the rectal cavity.

V. RELATIVE CONDITIONS IN MALE AND FEMALE.

The different divisions of the digestive tube in the female adult do not differ greatly from those described in detail for the male. The gross and microscopic arrangement of parts is the same in general plan. Esophagus and anterior crop are practically identical in structure in the two sexes. The posterior crop is much smaller in diameter in the female, its walls being crowded together by the surrounding fat and reproductive organs, but the walls themselves are similar in structure to those of the male. Ascending and descending intestine and rectum show no structural differences in the two sexes. There is, then, no great difference in the general plan and arrangement of the digestive organs of the male and female.

A gradual increase in the size of the posterior crop during the adult life of the cicada is noticeable. This increase in size is accompanied by a corresponding gradual decrease in the volume of the fat body. This results in the cavernous abdomen of the adult in its final period of existence, a condition especially striking in the male, but also observable in the female during its later history. Since the space necessary for the accommodation of the eggs is much larger than that required to store the sperms, this may account in part for the smaller average size to which the posterior crop attains in the female.

VI. DISCUSSION.

The relationship of parts in the digestive system of *Cicada orni*, as described by Dufour ('33), is unintelligible when the gross anatomy of the organs are alone considered. On the basis of what we have found in sections of the same system in *Tibicen septendecim*, however, it seems easy to homologize the structures described by Dufour with the corresponding ones in the present subject and to suggest further that the two much-coiled portions of the intestine figured for *C. orni* are connected by a labyrinth similar to the one described here as the "internal gland." Dufour did not study sections of his material and ordinary dissection methods would not reveal the relationships which are made plain by sections. If, in *C. orni*, there is any difference between the digestive systems of male and female, Dufour's figure is undoubtedly that of a female specimen. At any rate, the digestive apparatus is nearly identical with that of a female *Tibicen septendecim*. The one slight variation, namely, the point of connection between the ascending intestine and "internal gland," is easily explainable since the anterior portion of the posterior crop is usually much folded in these forms and the ascending intestine might be so placed between folds, and perhaps in addition have its wall actually grown fast to those of the ascending intestine, so as to appear to empty into the "ventricule chylique" (posterior crop). Examination of Dufour's figure of the digestive system of *Cicada orni* after studying sections of the same in *Tibicen septendecim* does not leave much doubt as to the similarity of the digestive apparatus in the two species.

VII. SUMMARY AND CONCLUSIONS.

1. There is a well-differentiated and continuous digestive tube in both male and female adult *Tibicen septendecim*.
2. The esophagus, which empties into the crop, shows no peculiarities of structure.
3. The crop is divided into two unequal parts (the anterior and posterior crops) by a constriction at the place where thorax and abdomen join.
4. The crop is partially obscured by a mass made up of ascending intestine and malpighian vessels. This mass has been called the "internal gland" (Lubbock '59).
5. The posterior crop is greatly enlarged, especially in the adult male, and its epithelium is extremely thin except at the extreme anterior and posterior ends.
6. The posterior crop empties into the ascending intestine which is yellow in color and runs forward until immediately dorsal to the anterior crop it winds about with the malpighian vessels to make the "internal gland."
7. The ascending intestine emerges from the internal gland and empties into the descending intestine.
8. The malpighian vessels are four in number and they empty into the digestive tube at the junction of ascending and descending intestines.
9. The descending intestine runs dorsally in a general posterior direction until it joins the rectum. The former is gray in color.
10. There is no degeneration of parts of the digestive tube of either male or female in the sense that any part ceases to be well organized or becomes disconnected from another part.
11. Nothing has been learned in connection with this study which throws any light upon the reasons for the peculiar life history of the cicada.

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IX. INDEX TO FIGURES.

- ac—anterior crop.
at—ascending intestine.
cm—circular muscles.
dt—descending intestine.
e—esophagus.
int—internal gland.
k—coil in ascending intestine.
kk—coil in descending intestine.
mt—malpighian vessels.
pc—posterior crop.
r—rectum.
x—junction of posterior crop with ascending intestine.
y—junction of malpighian vessel and intestine.

EXPLANATION OF PLATES.

PLATE XXIII.

- Fig. 1. Semidiagrammatic representation of ventral aspect of digestive system based upon dissections and reconstructions from sections. 10X.
Fig. 2. The same viewed from the left side.

PLATE XXIV.

- Fig. 3. Diagram of the digestive organs showing the relationships of the various parts and the course of the food stream.
Figs. 4, 5, 6. Diagrammatic figures of cross sections in anterior crop region showing probable method of complication resulting in intimate relation between anterior crop and "internal gland." Cf. Figs. 6 and 9.

PLATE XXV.

- Fig. 7. Frontal section through internal gland and anterior part of descending intestine.
Fig. 8. Vertical section through floor of anterior crop.
Fig. 9. Transverse section through forward part of internal gland, anterior crop and descending intestine.

PLATE XXVI.

- Fig. 10. Sagittal section showing junction of esophagus with anterior crop.
Fig. 11. Section through extreme anterior portion of posterior crop showing details of cell structure.
Fig. 12. Same slightly posterior to Fig. 11.
Fig. 13. Same midway between extremities of posterior crop.

PLATE XXVII.

- Fig. 14. Section showing junction of posterior crop and ascending intestine.
Figs. 15, 16, 17. Transverse sections through different parts of ascending intestine showing different phases of digestive activity.

PLATE XXVIII.

- Fig. 18. Transverse section through descending intestine at its anterior end.
Fig. 19. Same, midway between its extremities.